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SOCIAL ORGANIZATION AND RECRUITMENT

ON THE ARENA OF SHARP-TAILED GROUSE

by

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A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "Social Organization and Recruitment on the Arena of Sharp-tailed Grouse", submitted by Arthur Blair Rippin in partial fulfilment of the requirements for the degree of Master of Science.

ABSTRACT

Gradual removal of territorial male sharp-tailed grouse from two widely separated arenas began in late February, 1969 near Wainwright, Alberta. As the number of males decreased, new males began to appear on both arenas in early March. Recruitment continued until early April and then ceased. The results showed that a significant portion of the male population consisted of non-territorial birds which were apparently juvenile. The latter were prevented from becoming members of the social unit on the arena by males already occupying territories there.

During March 1969, most territorial males on ten arenas in a 24 square mile area were marked. A program of successive centrifugal removal of males began April 3 on two of these arenas. New recruits failed, with three exceptions, to be attracted to the experimental arenas. The pattern of filling vacancies indicated a social arrangement where a central male was surrounded by three concentric rings of males. As males were removed from the center, the radii of these rings decreased and the arena became smaller while the original territorial arrangement was preserved. A hierarchy was suggested in which dominance ranks decreased radially outward from the center but males making up a ring were of similar dominance.

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TABLE OF CONTENTS

ABSTRACT

ACKNOWLEDGEMENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION	1
STUDY AREA	4
METHODS	7
Procedure, 1968	7
Procedure, 1969	9
RESULTS and DISCUSSION	14
The Arena	14
Recruitment	19
Social Organization	33
Arena BL	35
Arena Apt	43
CONCLUSION	54
LITERATURE CITED	55
APPENDIX I	59

LIST OF TABLES

Table 1.	The sex and age of sharp-tailed grouse trapped or shot while attending arenas in autumn, 1969, near Wainwright, Alberta	22
Table 2.	Ages of male sharp-tailed grouse captured on arenas near Wainwright, Alberta in 1968 and 1969.....	29
Table 3.	Markers on male sharp-tailed grouse which attended Arenas BL and Apt during spring 1969, near Wainwright, Alberta	39

LIST OF FIGURES

Fig. 1.	The study area near Wainwright, Alberta	5
Fig. 2.	Aerial photograph of part of the study area. Circled light spots represent the locations of known arenas of sharp-tailed grouse	8
Fig. 3.	Markers placed on sharp-tailed grouse for individual identification near Camp Wainwright, Alberta	10
Fig. 4.	Grid systems of stakes used in 1968 and 1969 as reference points in the mapping of territories of sharp-tailed grouse on arenas near Wainwright, Alberta	11
Fig. 5.	Results of removal and recruitment of sharp-tailed grouse on Arena GV during spring, 1969, near Wainwright, Alberta	25
Fig. 6.	Results of removal and recruitment of sharp-tailed grouse on Arena R during spring, 1969, near Wainwright, Alberta	26
Fig. 7.	Maximum numbers of males observed on arenas in 1968 and 1969, near Wainwright, Alberta	27
Fig. 8.	Territorial arrangement of male sharp-tailed grouse on Arena BL on April 4, 1969, near Wainwright, Alberta :....	38
Fig. 9.	Changes in territorial arrangement of male sharp-tailed grouse on Arena BL from April 4 to May 8, 1969, near Wainwright, Alberta	41
Fig. 10.	Maximum daily numbers of birds present on Arena BL from April 4 to May 8, 1969, near Wainwright, Alberta	44

Fig. 11. Time of arrival, removal, and return of males on Arena BL near Wainwright, Alberta	45
Fig. 12. Changes in territorial arrangement of male sharp-tailed grouse on Arena Apt from April 3 to May 5, 1969, near Wainwright, Alberta	47
Fig. 13. Hypothetical model showing the reaction of male sharp- tailed grouse to central vacancies in relation to the position they occupy on the arena	51

INTRODUCTION

Territorial and hierarchal systems have been postulated by Wynne-Edwards (1962) as being important in density regulation of most populations of wild vertebrates. Territoriality results in a parcelling out of the available habitat,...."placing a ceiling on breeding density and leading to the exclusion of the surplus adults if any" (Wynne-Edwards, 1962:164). Hierarchal systems in animal populations are based upon the dominance of one animal over another. Those individuals of higher rank in the system have better chances for survival than those lower. "The function of the hierarchy, in fact, is always to identify the surplus" (Wynne-Edwards, 1962:139). The existence of such a surplus population in passerine birds was suggested by Stewart and Aldrich (1951), Hensley and Cope (1951), and Rowan (1966) in their experimental removal of breeding birds. In the Tetraonidae, evidence for this hypothesis was drawn from work done on red grouse (Lagopus lagopus) (Jenkins, 1963; and Jenkins, Watson and Miller, 1963). These workers found that a substantial portion of the population was non-territorial, usually did not breed, and eventually died. Since then it has been found that non-territorial individuals became territorial and bred when vacancies were created by the removal of territorial birds (Watson and Jenkins, 1967 and Watson, 1967).

Among the Tetraonidae, the males of some species congregate at particular points in their habitat, arenas, to perform courtship displays and breed. Many studies have shown that the arena

consists of a system of individual territories (Lack, 1939; Hamerstrom, 1939; Evans, 1961; Lumsden, 1965; Robel, 1966; Kruijt and Hogan, 1967; and others). It has been suggested by some that there is also a hierarchal system on the arena (Hamerstrom, 1939; Scott, 1942; Evans, 1961; Koivisto, 1965; and others).

Sharp-tailed grouse (Pedioecetes phasianellus), being a lekking species, lend themselves to studies of territorial and hierarchal systems and the possible role these systems play in populations. Furthermore, much is already known about the life history and general biology of this species (Hamerstrom and Hamerstrom, 1951, 1960; Evans, 1961; Lumsden, 1965; and others).

The arena and the activity thereon have been investigated in this species by Evans (1961), and Lumsden (1965). They showed that more courtship and territorial activity occurred at positions toward the center of the arena than at the periphery; that birds occupying central territories seemed to be dominant over peripheral birds and were involved in a large majority of the observed copulations; and that a relationship between territory size and dominance existed.

The nature and function of this social system, timing and means of recruitment into it, the extent to which birds involved represent a stable unit within the population, and the existence of an associated reserve population remains unknown.

During 1968 and 1969 I undertook to investigate these problems in central Alberta through removal experiments on the arenas of

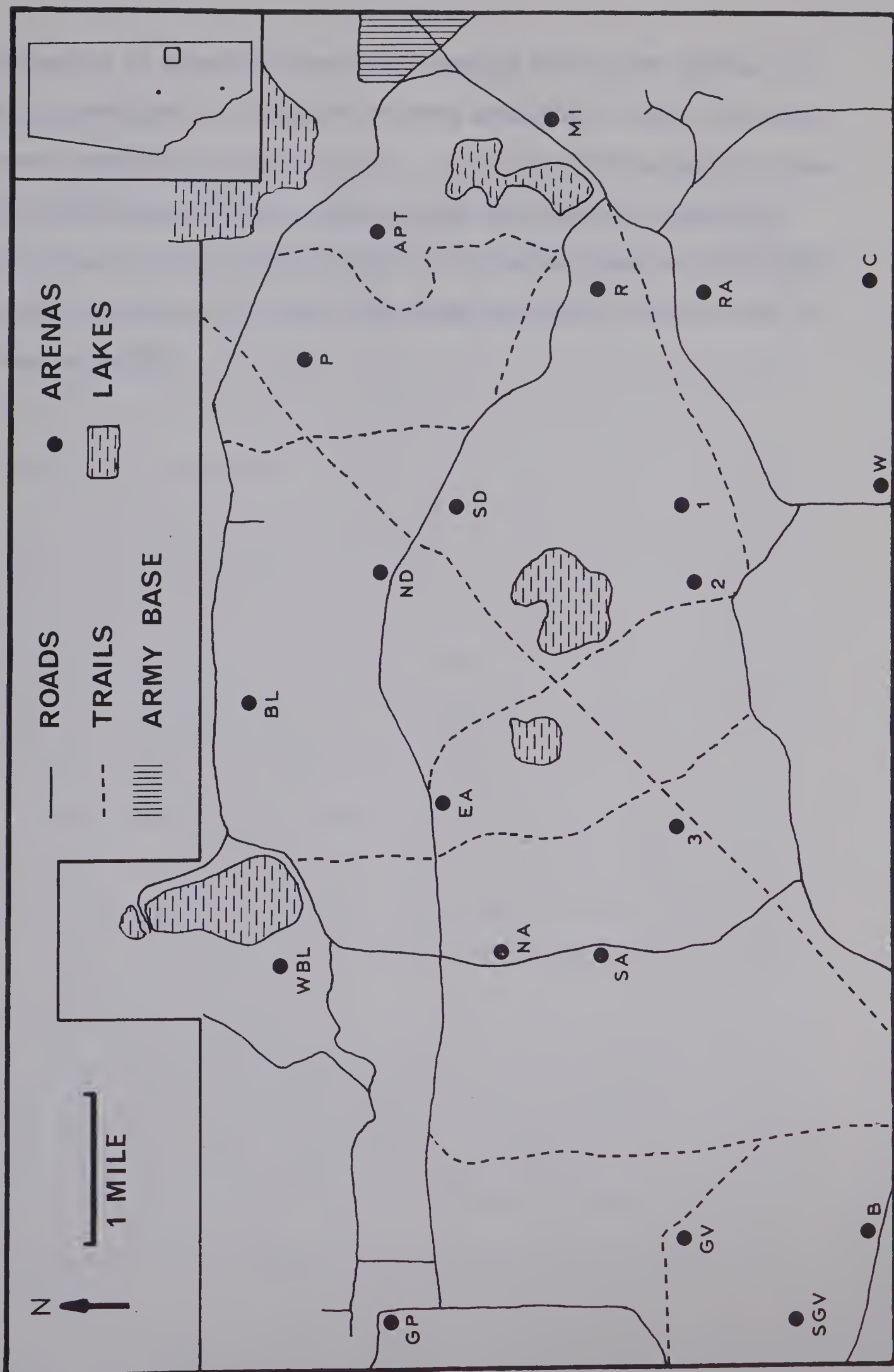
sharp-tailed grouse.

STUDY AREA

The study area included approximately 20 square miles in the northern part of Camp Wainwright, a military-training area located 126 miles southeast of Edmonton, Alberta (Fig. 1). The area is characterized by open aspen parkland which Bird (1961) describes as consisting of two distinct biotic communities; (a) the grassland community, and (b) the aspen forest community, with the percentage of aspen forest decreasing as one approaches the plains. In Camp Wainwright, the parkland is composed of approximately 50% grassland with native grasses such as porcupine grass (Stipa spartea var. curtiseta)*, rough fescue (Festuca scabrella), June grass (Koeleria cristata), and blue gramma grass (Bouteloua gracilis) as well as such exotic species as brome grass (Bromus inermis). Where topographic relief and edaphic conditions change, grass gives way to various shrubs such as buckbrush (Symphorocarpus occidentalis), snowberry (Symphorocarpus albus), wolf willow (Elaeagnus commutata), saskatoon (Amelanchier alnifolia), and chokecherry (Prunus virginiana). The forest community is represented by isolated groves of aspen (Populus tremuloides) growing to a height of approximately 20 feet. A major factor influencing the vegetation is fire which is used periodically by army personnel to reduce the chance of wildfire during military exercises. This has tended to maintain a greater

*Moss (1959) was followed for taxonomy of vascular plants.

Figure 1. The study area near Wainwright, Alberta.



proportion of grassland than would normally exist under present climatic conditions as evidenced by treed areas which exist in unburned areas immediately outside the Camp. The area is dissected with roads, and the movement of heavy army vehicles onto adjacent upland has left trails in the vegetative cover. Disturbed areas are susceptible to wind erosion of the very light sandy soils which underlie most of Camp Wainwright.

METHODS

Procedure, 1968

In this study it was necessary that the males on several arenas be trapped and marked for individual identification. In addition, it was necessary to have some means of determining the physical size and shape of individual territories on each arena.

Through annual surveys, the Division of Fish and Wildlife for the Province of Alberta had located seven sharp-tailed grouse arenas in Camp Wainwright prior to 1968. It was found that the location of known arenas coincided with light spots on aerial photographs of recently burned areas (Fig. 2). Using this fact, six additional arenas were located first on photographs and then in the field. Another 22 arenas were found by searching open elevated areas for flattened vegetation, droppings, and feathers, and by following sounds made by displaying males to their source.

Trapping and marking methods were tested during the period from May 4 to June 4. Males on seven arenas were trapped using Miller-type (Dzubin, 1965) and custom made (Schmitke, 1962) cannon net traps. The number and position of nets varied to ensure best coverage of specific arenas.

Each bird was individually color-coded with leg bands made of "Darvic" plastic; in addition, each carried a numbered aluminum leg band. All birds from a specific arena received a strip of "Saflag" fabric of specific color. These strips were threaded through the prepatagium of the left wing. The free ends were reflected over

Figure 2. Aerial photograph of part of the study area. Circled light spots represent the locations of known arenas of sharp-tailed grouse.



the dorsal aspect of the wing and stapled together (Fig. 3). These markers were visible on birds in flight and hence identified flushed birds with specific arenas.

Techniques for observing and mapping were tested from May 30 to June 12. Territories of males on six arenas were mapped with the aid of a square grid of colored stakes driven into the arena at ten foot intervals (Fig. 4). Mapping was done from a blind placed at the edge of the arena. The shape and size of specific territories were determined by observing movements and interactions of individual males with others on the arena in relation to the grid of stakes.

To determine the distribution of sharp-tailed grouse during the summer, the study area was systematically traversed throughout July and August of 1968 by a man on a Honda trail bike. The locations at which all marked and unmarked grouse were flushed were plotted on a map of the study area.

Procedure, 1969

To determine the nature, stability, and function of the social organization on the arena and the existence of a possible, non-territorial, reserve population, vacancies in the social system were created artificially by removing territorial male sharp-tailed grouse from specific arenas during the period of spring display.

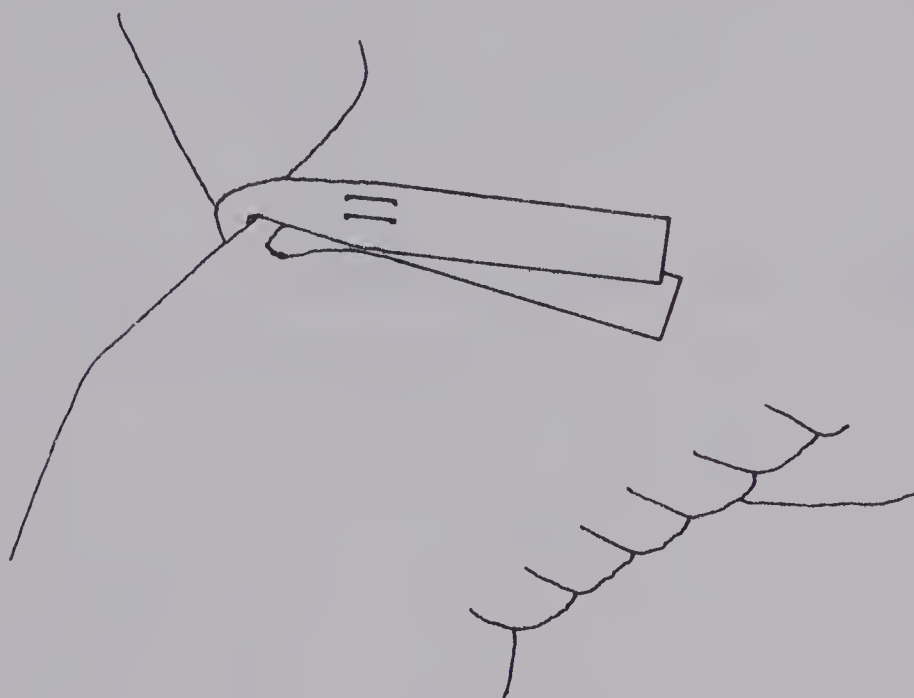
To determine whether recruitment would take place during spring if vacancies were created on the arena, removal experiments

Figure 3. Markers placed on sharp-tailed grouse for individual identification near Camp Wainwright, Alberta.

A.



B.



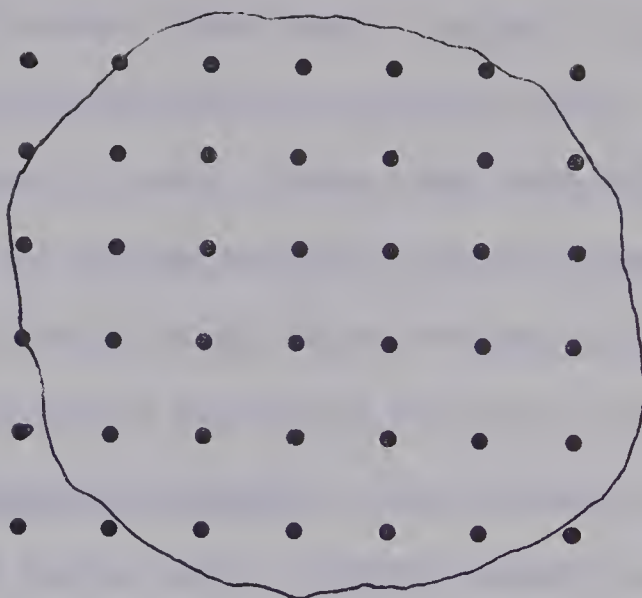
C.







- A. SAFLAG WING MARKER
- B. WING MARKER INSERTED
- C. DARVIC LEG BAND

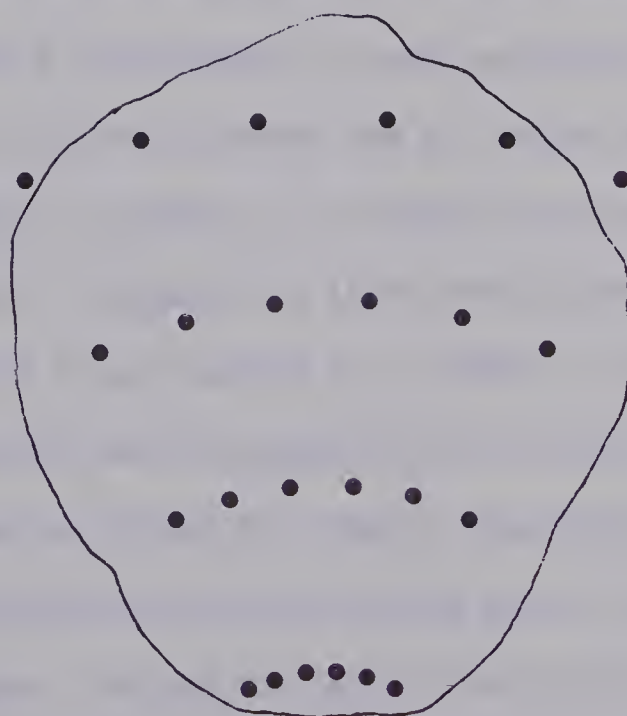
Figure 4. Grid systems of stakes used in 1968 and 1969 as reference points in the mapping of territories of sharp-tailed grouse on arenas.

1968



-  - BLIND
-  - STAKE
-  10 FEET
-  EDGE OF ARENA

1969



were initiated in early March, at the time when males began daily attendance at the arenas. From March 1 to April 10, males were gradually removed from two widely separated arenas, each of which originally supported 13 birds. These birds were either shot with a .22 caliber rifle or trapped in walk-in traps (Appendix 1) and killed with chloroform. The age of all birds removed was determined from feather measurements after the method described by Wishart (1969) for pheasants (Phasianus colchicus). The interval between removals varied from one to twelve days. Numbers removed on any one day varied from one to five, always leaving at least three males at each arena. The date of removal as well as the number removed and remaining were recorded for each arena.

To study the social organization on the arena as well as the nature and means of recruitment, it was necessary to have an area where all arenas had been located and all males thereon had been marked. Therefore, in March, a 12 square mile area containing ten arenas was chosen. The males on these arenas were trapped in walk-in traps (Appendix 1) and marked as in 1968. To aid in mapping of territories, a blind and fan-shaped grid of stakes (Fig. 4) were placed on two arenas chosen for removal experiments. The blind was entered by the observer in early morning prior to appearance of any birds on the arena. During the period from April 6 to May 8, a program of successive removal was undertaken in which the male holding the most central territory and usually the most active, was removed. Birds were removed at a rate of one every two days from

each arena until all males were eliminated. To show changes in the relative positions of territories on the arena, resulting from removal of central birds, maps were drawn of all territories before and after each removal. A record was kept of the number present on the arena, time taken for birds to return after shooting, time taken to fill vacancies, female activity, copulations, and changes in behavior.

Statistical tests used in the discussion were taken from Steel and Torrie (1960) and the 5% level of probability was chosen as the level of significance.

RESULTS and DISCUSSION

The Arena

Sharp-tailed grouse presently occupy most of the "open" country of north-central North America. They occur in many types of habitat; from desert sage in northern desert areas, oak savannah in the east, brush-grassland and parkland of the northwest, to openings in the boreal forest of northern Canada and Alaska (Aldrich, 1963).

Male sharp-tailed grouse congregate at particular points in their habitat to perform courtship displays in groups. Communal displays of this type are known in other tetraonids as well. Authors describing the behavior of tetraonids and the display areas used by males, have used terminology which has lead to some confusion. Areas used for display by North American tetraonids have generally received names that refer to some part of the display of a particular species. For example, part of the display of male sage grouse (Centrocercus urophasianus) consists of strutting, hence, the area used for display by males of that species is called a "strutting ground" (Scott, 1942; Lumsden, 1968). A "booming ground", the name given to the display area used by greater prairie chickens (Tympanuchus cupido), is derived from the booming sound produced by displaying males (Hamerstrom, 1939; Lumsden, 1965). The area used for display by male sharp-tailed grouse is commonly referred to as a "dancing ground" (Evans, 1961) because males appear to "dance" while displaying. In my opinion, this type of nomenclature can be misleading. The nomenclature used by

workers in Europe and the British Isles is, perhaps, more meaningful. Male black grouse (Lyrurus tetrix) also perform courtship displays in groups. The area used for communal display is generally referred to as a "lek" (Kruijt and Hogan, 1967) or an "arena" (Armstrong, 1947; Hjorth, 1968). The term "lek" has also been used as a verb with reference to the complex behavior and the performance of this behavior by males on the display area (Wynne-Edwards, 1962). In this discussion the term "lek" will be used as a verb with reference to the type of behavior shown by males belonging to that group of tetraonids in which males congregate at particular points in their habitat to perform courtship displays in groups. The term "arena" will refer to the area of habitat on which these males display.

Sharp-tailed grouse arenas tend to be located on open, dry, elevated sites (Hamerstrom, 1939; Ammann, 1957; Evans, 1961; Lumsden, 1965). Ammann (1957) found that 47% of 160 sharp-tailed grouse arenas were located on knolls, ridges, or slight elevations; 4% in depressions; and 49% on level ground. He suggested that the lack of suitable elevated sites in the area studied was the reason for one-half the arenas being on level ground. On one study area, Evans (1961) found a majority of the arenas on open elevated sites and suggested that the location of arenas was determined mainly by topography and vegetative cover. In a study of habitat requirements for sharp-tailed grouse, Ammann (1957) evaluated physical aspects of vegetative cover on various habitats where sharptails

occurred and found that the area with 20 to 40% woody cover - that is, trees and shrubs, contained most birds. Arenas were usually found in the most open part of the habitat. Therefore, it appears that sharp-tailed grouse require a fairly open habitat and that the most open part of the habitat, usually an elevation, is chosen for the arena.

Of 36 arenas found in Camp Wainwright, 32 were located on open, dry, elevated sites, while three were on level ground and one was on an elevation which had a heavy shrub cover. Because of the rolling nature of the topography in Camp Wainwright, it appeared that there was an abundance of elevated sites suitable for arenas. On the 24 square mile study area (Fig. 1) an attempt was made to determine whether arena sites were chosen in the most open part of the habitat. On aerial photographs, circles of one-half mile radii were drawn around arenas and around random points on the study area. The aspen cover within these circles was calculated. No significant difference could be found between the aspen cover around arenas and around random points. However, when Ammann (1957) analysed the cover around arenas, he considered shrub cover to be equivalent to tree cover. There were no data regarding shrub cover on my study area. Therefore, one can only suggest that if shrub cover is not important in the selection of arena sites, arenas on the study area were not necessarily located in the most open part of the habitat.

It was found that arenas on the study area tended toward a

statistically significant uniform distribution. If suitable elevated sites are abundant, which they seem to be, and arenas are not located in the most open part of the habitat, why are the arenas uniformly spaced? Little is known about the timing and means of establishing new arenas. Hamerstrom and Hamerstrom (1951) suspected that new arenas were established during autumn but evidence is lacking. Following are some suggestions which may account for the spacing of arenas.

One hypothesis is that the establishment of one arena influences the position of others around it. Schwartz (1945) suggested that each prairie chicken arena had a sphere of influence, the limits of influence determined by the distance and direction from which the sound made by displaying males was audible. If this is the case, then sound produced by displaying male sharp-tailed grouse may serve as a spacing mechanism in much the same way as male passerines use song to space themselves (Smith, 1966). It has been suggested that drumming of ruffed grouse may serve to space the males (Eng, 1959). The sound produced by displaying male sharp-tailed grouse is audible to the human ear over a distance of one mile under calm conditions. Therefore, it is conceivable that new arenas could be established at points where sound produced on adjacent arenas was minimal.

Studies of annual movements of sharp-tailed grouse in autumn, winter, and spring have shown that the arena forms the focal point for the activity of the lekking group of males over that part of

the year (Hamerstrom and Hamerstrom, 1951; Ammann, 1957). These authors have shown with marked birds, that the lekking flock associated with a particular arena has a potential daily cruising radius of about one mile but usually it is about half of this for much of the year.

To determine the distribution of lekking males while off the arena during summer, the points where marked males were flushed in 1968 were plotted on a map of the study area. Of 37 points where marked males were flushed, 97% were within one half mile of the arena on which they were marked the previous spring. These results support the idea that lekking grouse remain in the vicinity of their arena over most of the year and that the arena is indeed the focal point of year round activity. The sedentary nature of lekking flocks has also been reported in black grouse. Robel (1967) found that marked lekking males had home ranges which included the area on which the arena was located.

The above data could also be interpreted as indicating that spacing of arenas results from the apparent sedentary nature of lekking male sharp-tailed grouse, that is, a home range is established by a newly formed lekking group prior to choosing an arena site. If the arena was always located near the center of the home range of the lekking flock and areas occupied by such flocks were not overlapping, then spacing of arenas would tend toward uniformity.

Recruitment

Moffat (1903 in Rowan, 1966) proposed that suitable habitat was parcelled out among pairs of birds and that a reserve of non-breeders existed. Thus any undue increase in numbers was prevented, keeping the breeding population at a relatively constant level through territorial behavior. This proposal was met with opposition by early biologists because they could see no evidence of a non-breeding, reserve population (Nice, 1941; Lack, 1944). However, the parcelling out of available habitat or territoriality in birds became the subject of many studies (Howard, 1920; Nice, 1941; Lack, 1944). Hinde (1956), in a summary of current ideas about territoriality in birds, suggested that territory may exert a "limiting effect" on population density in suitable habitat. Wynne-Edwards (1962) generally accepted Moffat's ideas that density regulation in populations of animals may result from social behavior of its members. He proposed that through "epideictic displays", animals, in effect, were able to assess their population density and stimulate responses to hold it at or restore it to an optimum. Over exploitation of vital resources, food being most important, was avoided by substituting conventional goals to take the place of actual food and he proposed that through territoriality and hierarchal systems, animals could identify and exclude any surplus from the breeding stock. This theory has also been criticized (Lack, 1966; among others). However, recent studies on territorial birds have suggested that surplus non-breeders do exist

in some bird populations (Stewart and Aldrich, 1951; Hensley and Cope, 1951; Rowan, 1966). When territorial passerine birds were removed, the vacancies were rapidly filled by new members. However, they found no conclusive evidence that replacements were actually non-territorial prior to replacement. The best evidence for the existence of a non-breeding reserve comes from the work done on red grouse by Watson and Jenkins (1967). The population studied, contained many marked birds. It was reported that breeding always resulted in the production of more birds than stocked the area the following spring. A substantial portion of the population was found to be non-territorial. By removing birds at various times of the year, Watson and Jenkins found that members of the non-territorial population occupied the vacancies that were created. In cases where paired, territorial males were removed, males from the non-territorial population moved into the vacancies and mated with the resident females. They concluded that the size of the breeding stock was determined by territorial behavior because only territory owners bred. The owners, by being territorial, created a group which was unable to become territorial as long as the owners were present.

In the case of lekking species of birds, there is little evidence to support the idea that a non-territorial surplus may exist. The timing and means of recruitment of new members into the lekking group is poorly understood. There is some evidence that juvenile males appear on arenas with lekking flocks during autumn.

Hamerstrom and Hamerstrom (1951) observed eighteen males displaying on September 25, 1948, three of which were judged to be juveniles. Ammann (1957) reported that juvenile males were trapped on arenas in autumn. Autumn trapping on arenas in my study area during 1969 resulted in capturing several juvenile birds (Table 1.). Birds were considered juvenile if they retained the outer two primaries where adults molted these two feathers (Taber, 1969). It was therefore apparent that birds of the year attended the arena in autumn but there was no evidence that they established territories and became members of the lekking flock at that time. Lekking flocks seem to remain as cohesive units during winter (Hamerstrom and Hamerstrom, 1951; Ammann, 1957). Age ratios in winter flocks are not well documented nor is it known whether juveniles appearing on the arena during autumn remain with lekking flocks throughout winter. However, if juveniles which attend the arena in autumn become members of lekking flocks, perhaps the exclusion of the non-territorial population, mainly juvenile, occurs at that time.

Most studies on lekking species of birds have been conducted during the spring display period and the existence of a territorial system on the arena has been well documented. Although males have been observed on arenas periodically during winter, daily attendance does not begin until early spring (Evans, 1961; Lumsden, 1965). On my study area, daily attendance began in early March. However, there was some variation among different arenas. When males begin daily attendance, there is a high frequency of fighting

Table 1. The sex and age of sharp-tailed grouse trapped or shot while attending arenas in autumn, 1969, near Wainwright, Alberta.

Date	Adults		Juveniles		Total
	male	female	male	female	
Aug. 17-26	5	0	0	0	5
Sept. 27	2	0	1	0	3
Oct. 3-8	4	1	5	1	11

and an apparent lack of fixed spatial relationships among the males when compared to the low frequency of fighting and fixed territory boundaries characteristic of the breeding season (Hamerstrom and Hamerstrom, 1951; Evans, 1961). Whether recruitment of new members into lekking flocks takes place during the period of spatial instability is not known. Age ratios of males on arenas during the breeding season are poorly documented because of inadequate aging techniques and because few workers have attempted to obtain ages of the birds under study. Therefore, it is difficult to determine the time of occurrence of annual recruitment of juveniles into lekking flocks.

Most spring studies make no reference to a surplus, non-territorial population. However, Robel (1969) was able to follow movements of male black grouse equipped with radio transmitters. He found that among the males there was a lekking group and a non-lekking group during spring. Although his data on age ratios of non-lekking flocks were incomplete, Robel felt that they were composed largely of juveniles.

If such non-lekking groups of males exist in populations of sharp-tailed grouse, what determines the number of males allowed to establish territories on the arena? Social behavior may play an important role in this regulation, as suggested by Wynne-Edwards (1962). It is difficult to determine which aspects of social behavior may be involved and how they could act to prevent surplus males from establishing territories on the arena. Perhaps lekking

males, by being territorial, are creating a group which is unable to become territorial as long as territories are maintained by the owners' presence. To test this hypothesis, males were gradually removed from two widely separated arenas during the spring of 1969. Recruitment of new members did occur on both experimental arenas (Figs. 5 and 6). Because of recruitment, 26 males could be accounted for from each arena at the end of the experiment, whereas initially only 13 males were present. The number of males on Arena GV prior to 1969 was unknown but a maximum of 15 were present on Arena R, based on counts conducted in 1968. From 1968 to 1969 there was a general decline in the number of males attending arenas on the study area (Fig. 7). Therefore, it is unlikely that there would have been more than 13 males present at any one time had the original birds not been removed from either Arenas GV or R. The amount of recruitment observed on Arenas GV and R may indicate that a substantial portion of the male population is non-territorial. However, none of the males initially present or recruited were marked and it is not known if the recruits were non-territorial prior to their appearance on Arenas R and GV; they could have been territorial on adjacent arenas. Over the period that males were being removed from Arena R, males were being trapped and marked on four adjacent arenas. These males would have been available for recruitment onto Arena R if inter-arena movements occurred. However, no marked birds were recorded on R and counts on neighboring arenas remained relatively constant suggesting that recruits probably come from a

Figure 5. - Results of removal and recruitment of sharp-tailed grouse on Arena GV during spring, 1969 near Camp Wainwright, Alberta.

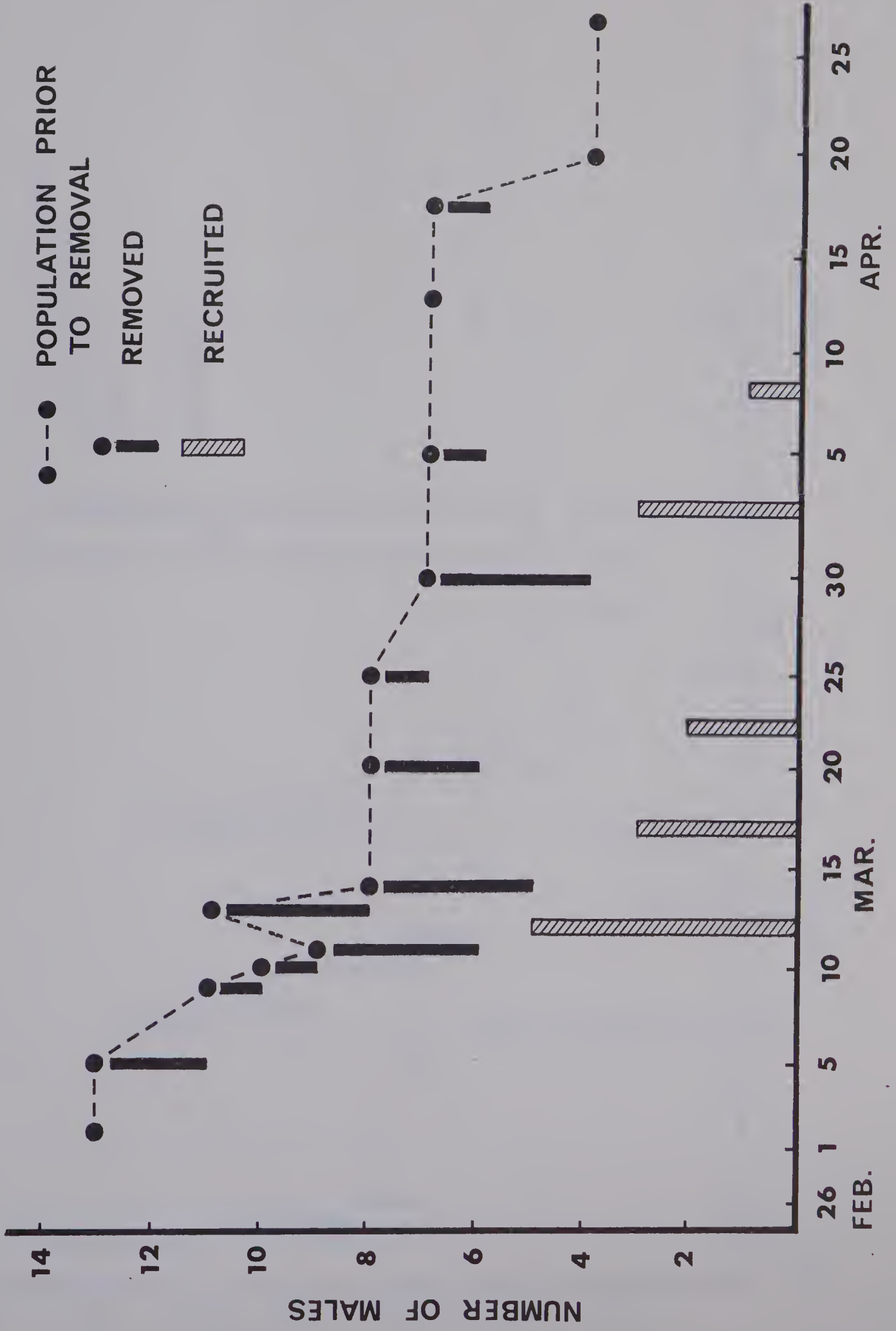


Figure 6. Results of removal and recruitment of sharp-tailed grouse on Arena R during spring 1969 near Wainwright, Alberta.

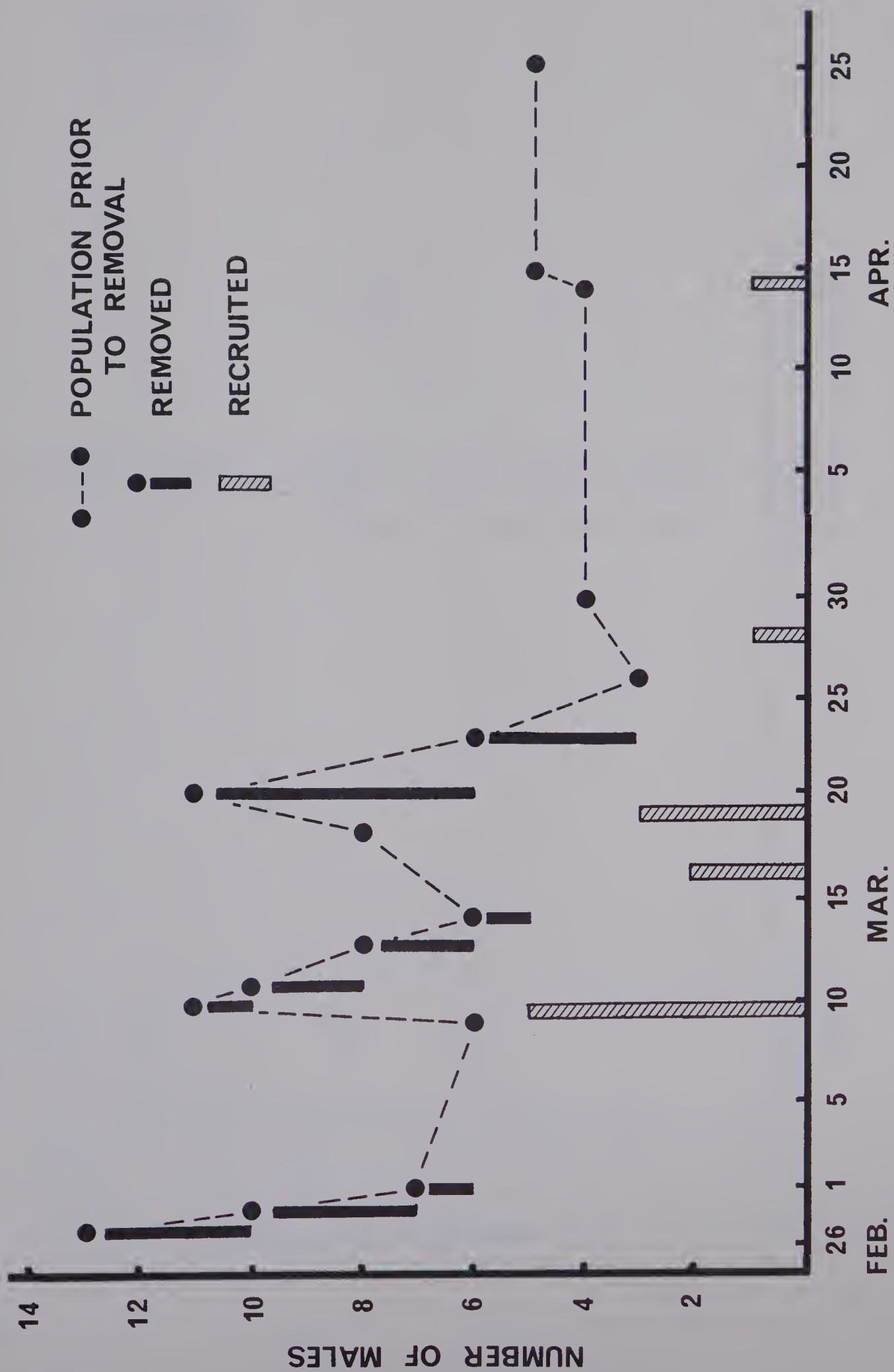
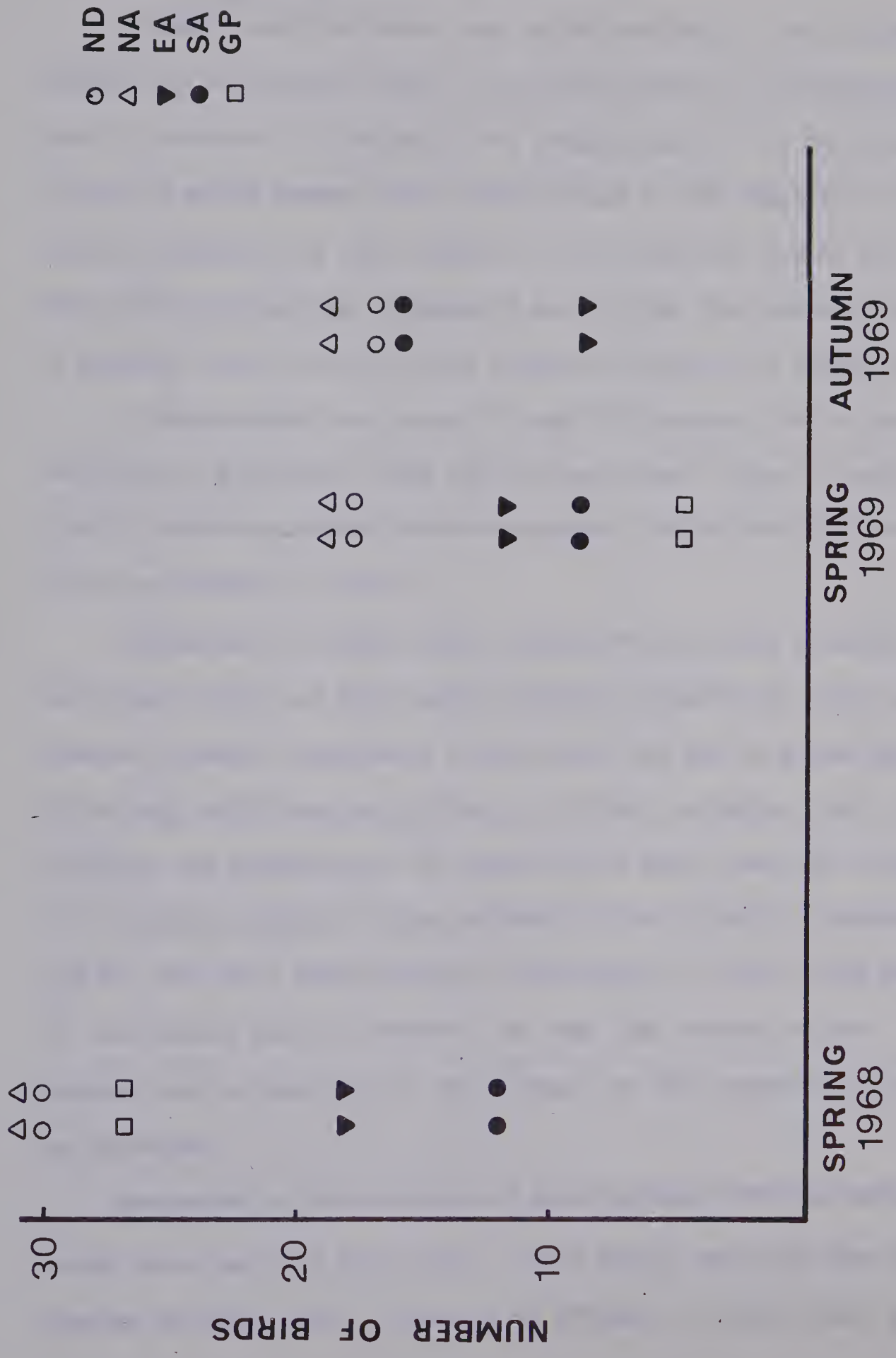


Figure 7. Maximum numbers of males observed on arenas in 1968 and 1969 near Wainwright, Alberta.



non-territorial segment of the population.

Because recruited males were indistinguishable from original members of the lekking group, it was not possible to determine the age of recruits. To determine the probable age of the recruits, age ratios of males removed from Arenas GV and R were compared to age ratios obtained from other arenas on the study area (Table 2). The greater proportion of juvenile males taken from Arenas GV and R suggests that recruited males probably consisted of juveniles.

If recruitment onto Arenas GV and R originated from a non-territorial population, then why did recruitment cease in early April? Several possible factors may have limited the time over which recruitment occurred.

The number of surplus males associated with each arena may have been finite and this number had been exhausted by early April. However, removal experiments during April and May on Arenas Apt and BL failed, with three exceptions, to attract recruits. One of the recruits was unmarked and two marked birds came from other arenas. If a similar surplus of males existed in the vicinity of Arenas Apt and BL, one would expect similar recruitment to result from removal of territorial males. However, the time that vacancies were created may be important to recruitment, so this hypothesis can not be rejected.

The number of non-territorial males present over the entire study area, may have been finite. This supply may have been exhausted by early April. There is no evidence to refute this possi-

bility. However, an estimation of the total population of adult birds was conducted for the area around five arenas on which males were marked. Seventy-seven of 99 territorial males were marked during spring, 1968. If a one to one sex ratio is assumed among adults, then the population in the vicinity of the five arenas would consist of 198 individuals. During the following summer, 113 adults were sighted in the vicinity of the five arenas while traversing the study area on a Honda trail bike. Of these, 23 were marked. Assuming an equal chance of sighting marked as well as unmarked adults, the Lincoln index (Overton and Davis, 1969) was applied to these data to obtain an estimate of the actual population around the five arenas during spring.

$$\begin{aligned} \text{Population estimate} &= \frac{\text{total marked} \times \text{No. sighted}}{\text{No. marked sighted}} \\ &= \frac{77 \times 113}{23} \\ &= 380 \end{aligned}$$

This estimate is considerably higher than the original estimate of 198 individuals, suggesting that a substantial portion of the population is non-territorial. However, because of the many assumptions involved in this calculation, the results may not be indicative of the actual situation.

Surplus males may have died by April. Watson and Jenkins (1967) and Watson (1967) found that most surplus red grouse died during winter and little recruitment occurred when vacancies were created in winter and early spring. Remains of some marked red grouse, which were known to have been non-territorial, were recovered during winter and found to be badly emaciated and heavily infested with parasites. However, red grouse and sharp-tailed grouse differ in food habits. Red grouse are generally monophagous, eating only heather (Calluna vulgaris) (Miller, Jenkins and Watson, 1966) and the surplus population were forced into areas where heather was lacking (Watson and Jenkins, 1967). Sharp-tailed grouse subsist on a winter diet of browse, berries, seeds of wild forbs, and will utilize grain when available (Ammann, 1957). There was no evidence that these types of food were unavailable on or near the study area. The possibility of starvation, therefore, is unlikely.

The well known effect of photoperiod on reproductive development in birds (Farner, 1964) may be insufficient in itself to elicit a strong territorial drive in male sharp-tailed grouse. Darling (1952) states that social stimulation is necessary in certain birds to complete sexual development. Fighting and singing are forms of social stimulation and have indirect survival value as aids to development of reproductive condition. If non-territorial sharp-tailed grouse males exist, they are presumably denied the stimulation that comes from occupying a territory on the arena and may not

have attained the degree of sexual development necessary to establish or maintain a territory by April.

Recruitment onto Arenas GV and R ceased at approximately the time spatial relationships among males became stable on Arenas Apt and BL. Social organization both on and off the arena may have become very rigid and may have lead to the exclusion of any surplus from areas in the vicinity of the arena. Thus recruits would be unavailable to replace territorial members after spatial relationships stabilized. However, there is little evidence to show that a rigid social organization exists in lekking groups of sharp-tailed grouse while off the arena.

Further study is necessary to determine which of the above alternatives is most likely.

Results of removal experiments on Arenas GV and R have shown that replacement will occur in early spring when territorial males are removed from sharp-tailed grouse arenas. Recruits likely originate from a surplus non-territorial population which probably consists of juvenile males. Thus, such aspects of social behavior as territoriality and dominance ranks may be regulating the number of males allowed to become members of lekking flocks.

Social Organization

Individuals of every species of vertebrate have a cohesive social tendency to associate with others of the same species (Hunsaker and Burrage, 1969). However, within groups of animals, individuals have a tendency to keep others at a distance. The optimum distance beyond which there is no reaction, but within which individuals exhibit agonistic behavior toward one another is referred to as "individual distance" (Hediger, 1955). Early studies of domestic fowl have shown that equality does not necessarily prevail in these relationships (Masure and Allee, 1934). A dominance-subordination relationship is one of the most common types of relationship found in vertebrates. "In this type of relationship the behavior of both individuals may be described as agonistic. That of one individual consists of threat or actual fighting while the other individual remains passive or attempts to escape" (Scott 1956;217). In competition for the necessities of life, dominant individuals have prior choice (Wynne-Edwards 1962). Thus, a space in the habitat can become an external reference for dominance. "When the external reference for dominance is more or less fixed in space it is commonly spoken of as a 'territory'" (Marler and Hamilton, 1967:171). Territory, as used in animal studies, has been defined as any area which is defended (Noble, 1939). This definition makes no reference to function but is one of the few with universal validity (Hinde, 1956). In the case of lekking birds, however, the territory appears to facilitate pairing

and reduce interference. It is used exclusively for courtship and/or copulation (Höhn, 1953).

Observation of courtship and mating activity on display arenas of lekking species has lead to a number of differing opinions as to the nature of the social organization manifested. Some workers have reported that the majority of observed copulations were performed by males occupying territories near the geographic center of the arena (Hamerstrom, 1939; Evans, 1961; Robel, 1966; Kruijt and Hogan, 1967). However, variations in this general rule have been reported (Hjorth, 1966; Brown, *pers. comm.*). The reason for the central males having a major role in reproductive activity is poorly understood. Kruijt and Hogan (1967) have shown that the probability of a male black grouse copulating with a receptive female is proportional to the amount of time the female spends in that male's territory. They suggested that the female chooses the place of copulation and listed several possible reasons for the choice. Central males were found to display and fight more often than peripheral males. Females were seen to approach fighting males on several occasions. Central males also were thought to have better tactics for attracting females. Females seemed particularly attracted to squatting males. It was also felt that females could discriminate density of males and the center, being more dense with respect to males, determined where a female mated.

Scott (1942), in a study of sage grouse, reported that most matings which occurred on a particular arena were performed by one

male. He called that bird the "master cock". Evans (1961) used the concept of a "master cock" in his study of sharp-tailed grouse and assumed the "master cock" to be most dominant. He then based dominance relationships among other males on the arena on this assumption. Although a majority of the territorial boundaries remained very stable throughout the breeding season, there were instances in which locations of territories changed. Evans attributed the changes to a tendency for a male to either enlarge its territory or to shift to a position closer to the center, as defined by the territory of the "master cock".

Mating success may not be a consequence of dominance but of territorial arrangement on the arena, which, in turn, may be related to social organization within the lekking group. Thus, by observing shifts in positions resulting from removal of males, (i.e.), artificially creating vacancies in the territorial system, one may discover the nature of the social organization present. Ideally, vacancies should be created centrally on one series of arenas and peripherally on another because of apparent differences in territorial and mating activity at the center and periphery of an arena. However, because time was limited, only the former was done on two different arenas (BL and Apt).

Arena BL

At the initiation of removal experiments on Arena BL there were 14 marked and five unmarked males present. The marked males

included 13 which had been captured and marked on Arena BL and one which had been marked on Arena ND (Fig. 1) during March. The unmarked males included two which could be identified by individual physical characteristics. One had been injured in a trap and absence of feathers on the top of its head was obvious. The second could be identified by very dark feathers in the malar region. The other three males had no obvious distinguishing marks and were identified only by the positions they occupied relative to marked males on the arena.

Mapping of territories on this arena was begun on April 4. Evans (1961:53) describes a method used to determine the position of territorial boundaries. "When paired interactions occurred, both rivals involved normally engaged in threat postures, directed at each other from stationary positions. The location on the dancing ground of these paired interactions are assumed to indicate the position of the territorial boundary between adjacent cocks". A minimum of 35 interactions involving a particular male were necessary to obtain a reliable estimate of the territory size and shape for that male (Evans, 1961). Maps of territories were drawn before and after each male was removed. The time allowed for territory mapping prior to removal on Arena BL was limited to an average of 58 minutes each morning. This situation rarely allowed observation of 35 interactions necessary to delineate the size and shape of territories of all males on the arena. Therefore, the mapped territories can not be considered precise with respect to

boundary locations. However, the relative positions of males on the arena can be effectively used to show movements resulting from the creation of vacancies. To show the relative positions of each male which occupied a "closed" territory, i.e., those which were entirely surrounded by territories of other males, the mean position of all observations of each male was plotted for each mapped territory. To show the relative position of males occupying "open" territories, a circle which conformed as closely as possible to the known boundaries was drawn in each territory. The center of each circle represented the relative position of males with "open" territories (Fig. 8). For convenience, males were designated by letters in the order they were removed (Table 3).

Male A was removed first from Arena BL because it appeared to be one of the most active males on the arena. The position occupied by A was also considered to be an approximation of the geographic center of the arena.

The original territorial arrangement on Arena BL is portrayed in Figure 8. The territory of A was surrounded by a ring of territories occupied by K, I, C, B, F, H, and D. K and I occupied territories which had peripheral boundaries defined by a dense stand of chokecherry, while C, B, F, H, and D occupied "closed" territories. This ring of territories was, in turn, surrounded by another partial ring consisting of the territories of R, P, G, N, T, O, S, and M. Most of these males occupied "open" territories. U, E, J, and Q occupied positions peripheral to the second ring.

Figure 8. Territorial arrangement of male sharp-tailed grouse on
Arena BL on April 4, 1969 near Wainwright, Alberta.

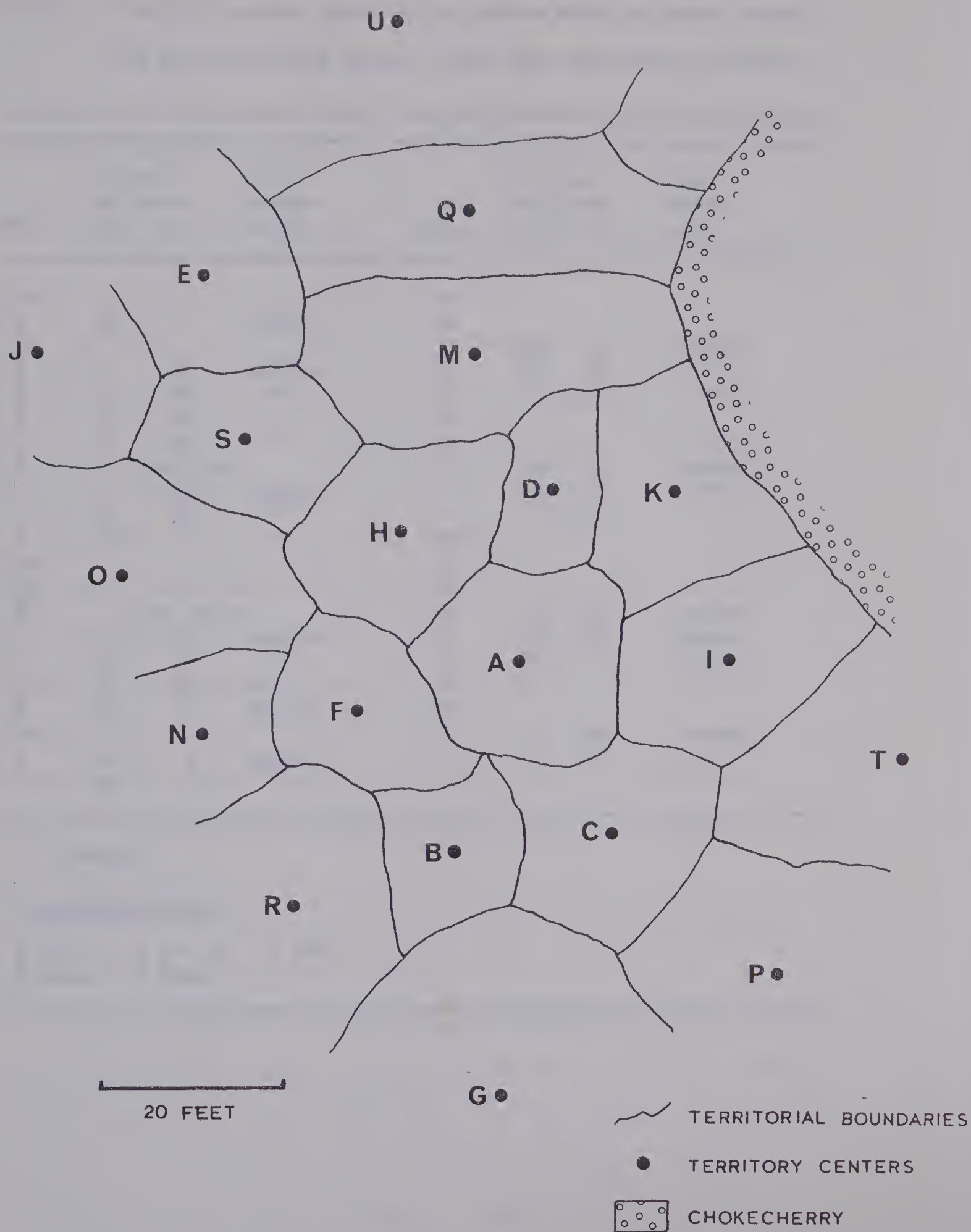


Table 3. Markers on male sharp-tailed grouse which attended Arenas BL and Apt during spring, 1969, near Wainwright, Alberta.

Male	Colored leg bands.		Wing marker color	Male	Colored leg bands		Wing marker color
	lft.	rt.			lft.	rt.	
A*				A*			
B	YB	G	purple	B*			
C*				C	WW	G	orange
D	G	WG	purple	D	GG	R	"
E	G	RY	"	E	G	YY	"
F	G	RW	"	F*			
G	G	RB	"	G*			
H		scalped		H	BW	G	orange
I	G	RR	purple	I	G	BB	"
J	G	RG	"	J	G	BY	"
K	RR	G	"	K*			
L*				L*			
M*				M*			
N		dark malar		N	G	YW	orange
O	G	YG	purple	O	R	GG	green
P	YY	G	"	P	BB	G	orange
Q	Y	RR	blue	Q*			
R	YW	G	purple	R*			
S*				S	G	BW	orange
T	GB	G	purple	T	R	GR	"
U	RW	G	"				

* unmarked

Colored leg bands

G green Y yellow R red
W white B blue

For convenience in the discussion, the rings of territories will be referred to as; ring 1, immediately surrounding the territory of A; ring 2, surrounding ring 1; and ring 3 which is only partial and consists of the territories of Q, U, E, and J.

Males were removed by shooting. Movements resulting through removal of males are pictured in Figure 9.

When A was shot on April 6, all other birds on the arena flushed and A was retrieved. The flock returned after 12 minutes and most males appeared in their former positions. B appeared in the vacancy while F, C, T, and G extended their territories laterally, that is, in an arc with the geographic center of the arena as origin, thus sharing the vacancy left by B. Display activity resumed with no obvious change. There appeared to be little fighting involved when B moved into the vacancy. From the map drawn on April 9 prior to the removal of B, it was apparent that Q had made an inward movement from ring 3 toward the geographic center and was then considered to occupy a position in ring 2. The inward movement of Q caused M, S, O, N, and T to shift slightly but none moved out of ring 2. All other males remained in their relative positions (Fig. 9).

After B was shot, the remaining males returned to their former positions and the vacancy was shared by all males in ring 2 through inward extension of their territories. No male could be considered central. Thereafter, males were removed from ring 1. When C was removed, F and I shared the vacancy. Between April 11 and 13, E

Figure 9. Changes in the territorial arrangement of male sharp-tailed grouse on Arena BL from April 4 to May 8, 1969 near Wainwright, Alberta.

= MALE REMOVED

= MOVEMENT AFTER REMOVAL

and D disappeared. M moved inward from ring 2 to take up the vacancy left by D in ring 1. The disappearance of E had no effect on males in rings 1 and 2. J and U shared the vacancy. When F was removed, G moved inward from ring 2 to take up the vacancy left in ring 1 and all others on the arena remained in their relative positions. The vacancies left when M and G moved inward were shared by males occupying positions in ring 2. Removal of G, H and I from April 15 to 19 had no effect on the relative positions of males in ring 2. On April 19, J, which formerly occupied a position in ring 3, appeared in the vacancy left when I was removed. On the same day, L, which was not known prior to that time, appeared in ring 3. Upon removal of J and K, L moved first into ring 2 and finally into the vacancy in ring 1 left by K. In addition, D, which had disappeared April 11, appeared in the vacancy left when L was removed. In effect, J, L, and D bypassed ring 2 to occupy central positions. Males in ring 2 retained their relative positions until April 29. Removal of males from the center and from ring 1 during the period from April 6 to 29 resulted in the contraction of ring 2. Although males in ring 2 converged on the center of the arena, they remained in their relative positions and as well, retained the circular configuration of the ring of territories. In effect, removal of males caused the arena to diminish in size while maintaining the original territorial arrangement. After April 29, the creation of central vacancies resulted in successive, individual, inward movement of males from ring 2. On May 8, the experiment was

terminated with the removal of all but one of the remaining males.

In general, recruitment to vacant areas was accomplished with little disturbance to other males on the arena. The intensity of interactions between a new occupant and surrounding males did not appear obviously different than between the former occupant and the surrounding males. During the experiment, males became increasingly more wary. However, at no point in removal was there any abrupt change in display activity.

Females were usually present at some time each morning throughout the experiment. Nine copulations were observed. These were performed by Q, N, M, R, and D (Fig 10).

The time taken for the lekking flock to return after shooting was variable (Fig. 11). The time taken to fill vacancies after return was also variable but the presence of females on the arena accelerated the process. If females returned with the lekking flock, vacancies were filled immediately. In instances where females did not return with the males, vacancies usually remained unoccupied until females appeared. In some cases, females failed to appear after shooting and vacancies remained unoccupied for at least one hour. On April 25, males failed to return after L was shot. However, the vacancy was occupied by D on April 28.

Arena Apt

Shifts in positions of territories resulting from the creation of vacancies in the territorial system on Arena Apt were, in most

Figure 10. Maximum daily numbers of birds present on Arena BL
from April 4 to May 8, 1969, near Wainwright, Alberta.

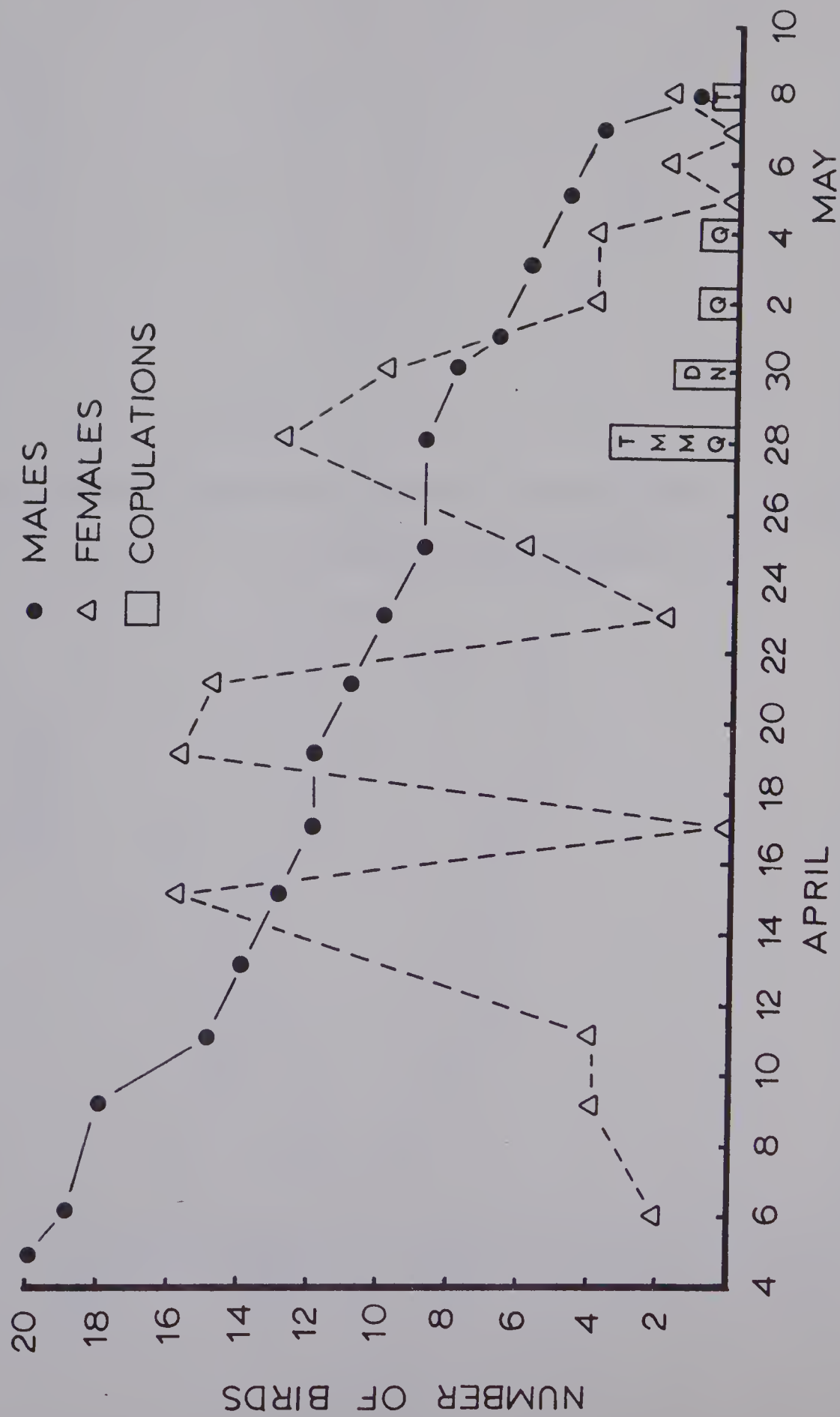
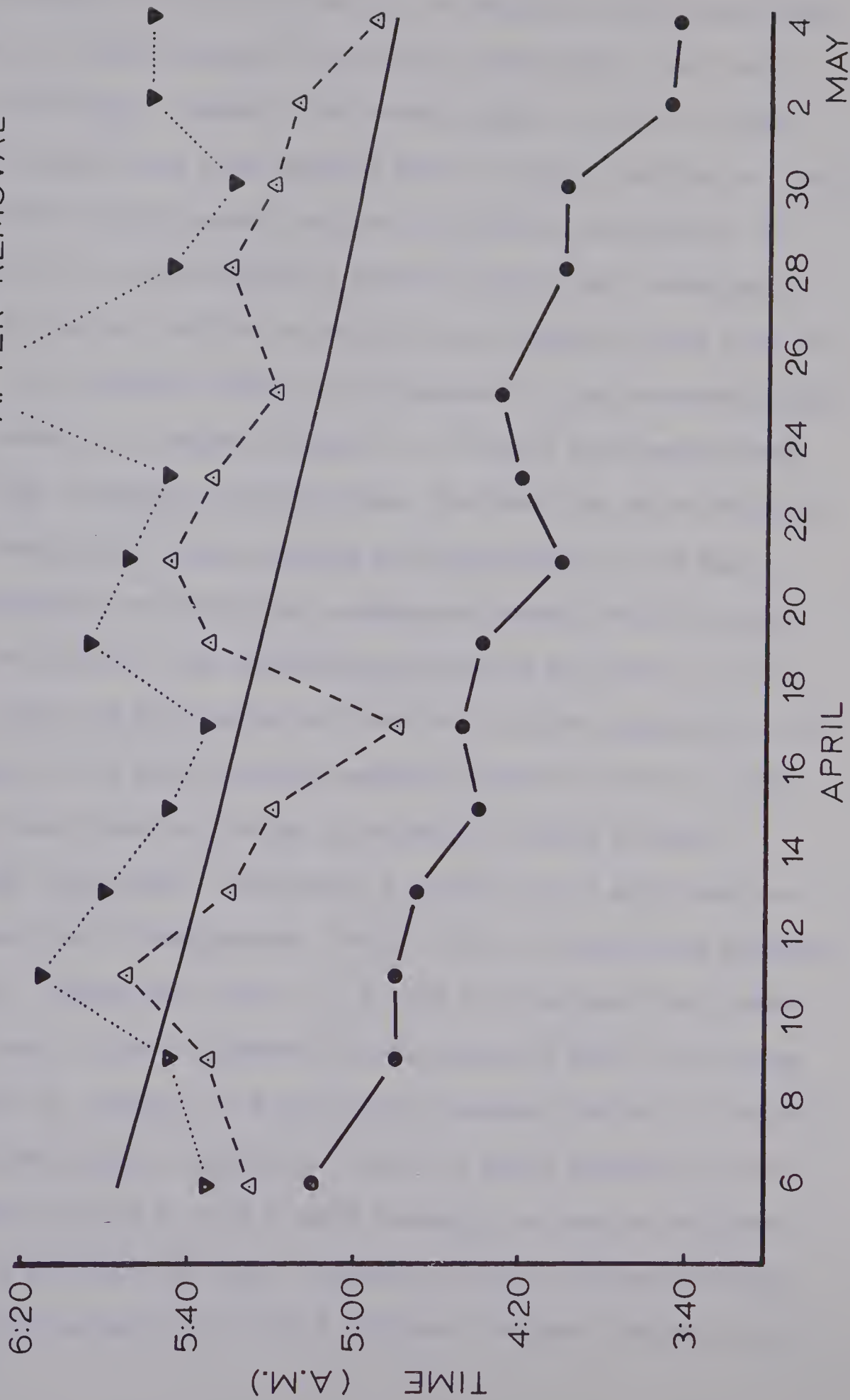


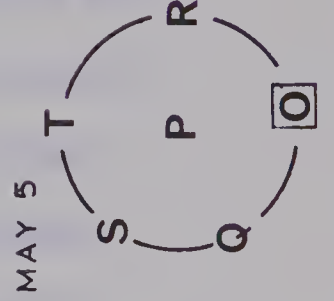
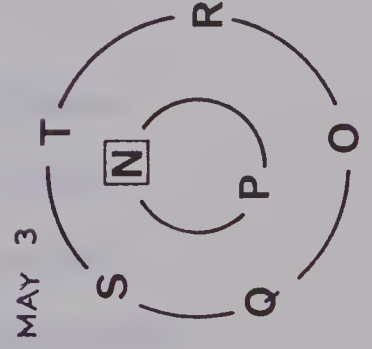
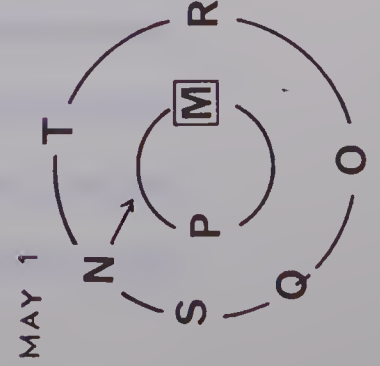
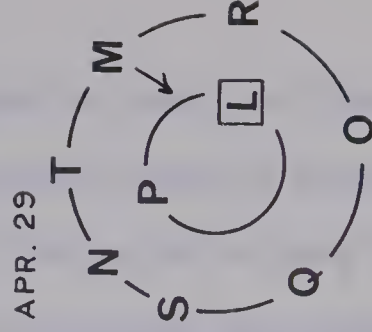
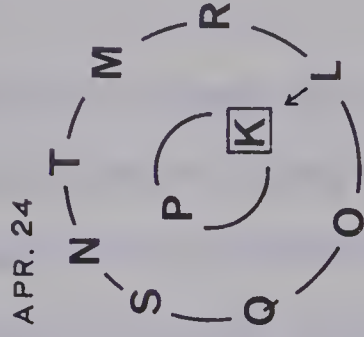
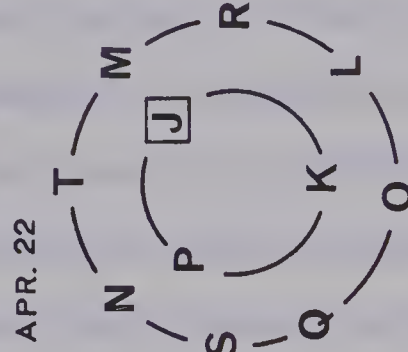
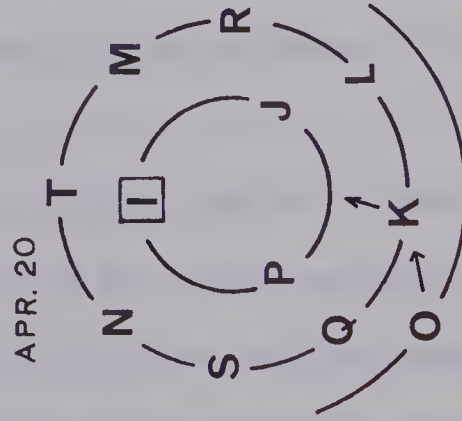
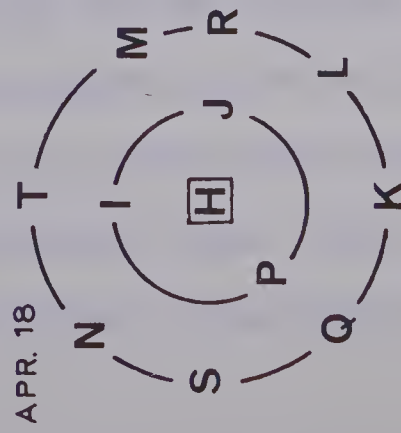
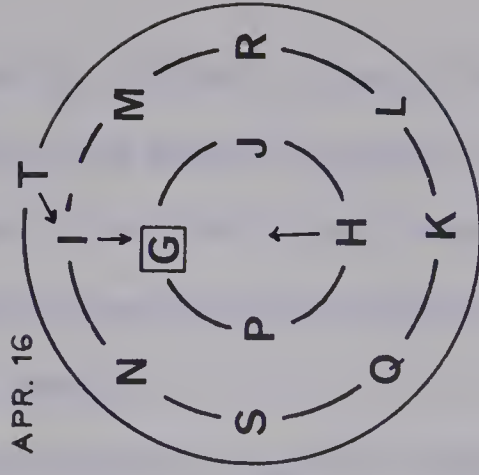
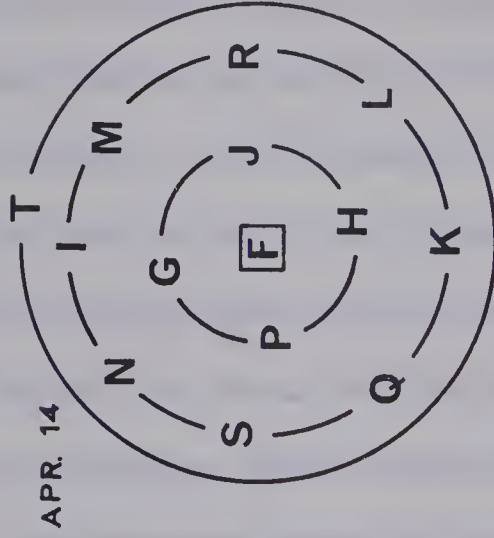
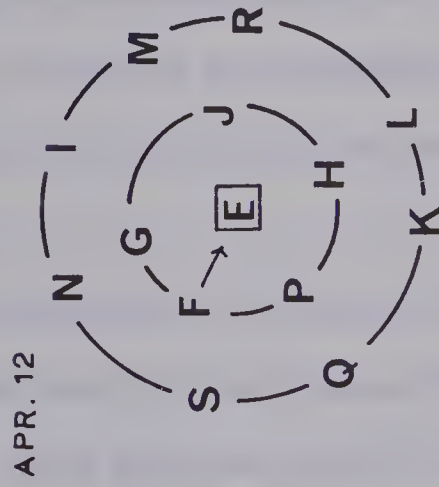
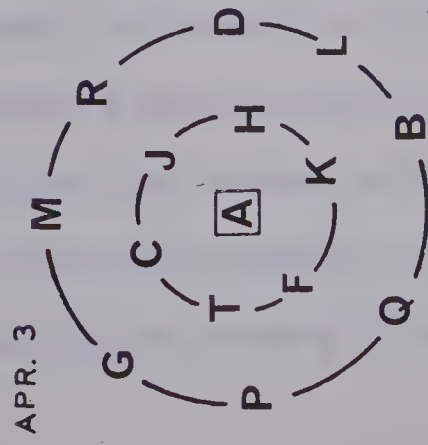
Figure 11. Time of arrival, removal, and return of males on Arena
BL near Wainwright, Alberta.

— SUNRISE
 ●—● ARRIVAL OF MALES
 ▲---▲ TIME OF REMOVAL
 ▼.....▼ RETURN OF MALES AFTER REMOVAL



cases, similar to those on Arena BL, but with some major exceptions. Eleven of 19 males present on Arena Apt during March, were captured and marked. However, when removal began on April 3, there were five marked and nine unmarked males occupying territories. None of the nine unmarked males could be individually identified. As on Arena BL, a male occupying a central position and appearing to be one of the most active on the arena, was chosen for the first removal. The original territorial arrangement, using the same criteria as on Arena BL, is shown in Figure 12. After A was removed there was a high frequency of fighting when the remaining males returned. Major territorial shifts occurred and because many of the males were unmarked, the territorial arrangement became very confusing. After the return of the remaining males when A was shot, S, E, I, and N, which had been marked on Arena Apt in March, appeared at the periphery of the arena and made several attempts to enter. Their advances were repelled through fighting and chasing by males occupying territories. From April 5 to April 12, B and D were removed and C and T disappeared. Major shifts in territorial positions resulted. During this time S, I, E, and N established territories on the arena. The arrangement of territories on April 12 is shown in Figure 12. Removal of E resulted in movement similar to the general pattern found on Arena BL, that is, F moved centrally to fill the vacancy, males in ring 1 moved laterally to take up the space left by F and males in ring 2 remained in their relative positions. Movements from April 14 to May 7 followed a pattern similar to that

Figure 12. Changes in territorial arrangement of male sharp-tailed grouse on Arena Apt from April 3 to May 5, 1969, near Wainwright, Alberta.



LETTERS POSITIONS OF MALES
 REMOVED MALE
 MOVEMENT AFTER REMOVAL

on Arena BL. Males in ring 2 tended to remain in their relative positions and moved centrally only when males in ring 1 were decreased to one. With each removal the males in ring 2 converged on the center keeping their relative positions, thus reducing the size of the arena.

The period of spatial instability on Arena Apt in early April may have been the result of social breakdown caused by removal, although removal after April 12 had little disturbing influence. It is probable that the males were still in the process of establishing territories in early April because four males previously marked on Arena Apt did not establish or re-establish territories until April 12. Also, during the period of instability, there were several instances where non-territorial males attempted to occupy vacancies and were driven out with much fighting by territorial males. This was not observed on Arena BL. Fighting and chasing was much more prevalent on Arena Apt than on Arena BL in early April.

Another factor that may have had an effect on the different spatial stability on Arenas Apt and BL is the age ratio of the males. The males on Arena BL consisted of 50% adults while 80% were adult on Arena Apt. Although the age structure of males within lekking flocks are poorly documented, there are instances where a few males, which were marked, have been seen on arenas for more than one season (Lumsden, 1965; Evans, 1969). Evans (1969) reported that five male sharp-tailed grouse, of ten which had been banded

on an arena in the spring of 1959, returned to the same arena the following spring and occupied approximately the same positions on the arena. The other five males were not seen on any of the neighboring arenas in 1960 and were presumed dead. It thus appears that once a male has become territorial it will maintain a territory for at least two seasons and probably for the duration of its life. Therefore, one could assume that all adults attending Arenas Apt and BL in the spring of 1969 had been territorial on those arenas the previous year. If that was the case, one would expect the flock with the highest ratio of adults to return to their arena the following spring and settle territorial boundaries with a minimum of fighting and chasing because adults would be familiar with the positions of the territorial boundaries. However, this was not the case, and the opposite was true. The reason for delay in spatial stability observed on Arena Apt, therefore, remains unexplained.

On the basis of observed shifts in positions of territories resulting from the creation of vacancies in the territorial system on both Arenas BL and Apt, males were divided into three groups; (a) "central" males, consisting of the central male and those whose territories formed ring 1; (b) "intermediate" males, which occupied positions in ring 2; (c) "marginal" males, which occupied positions in ring 3. Each group of males reacted differently to the creation of central vacancies. Central males generally rearranged their territorial boundaries to share vacancies with other central males. Except for the period of instability on Arena Apt,

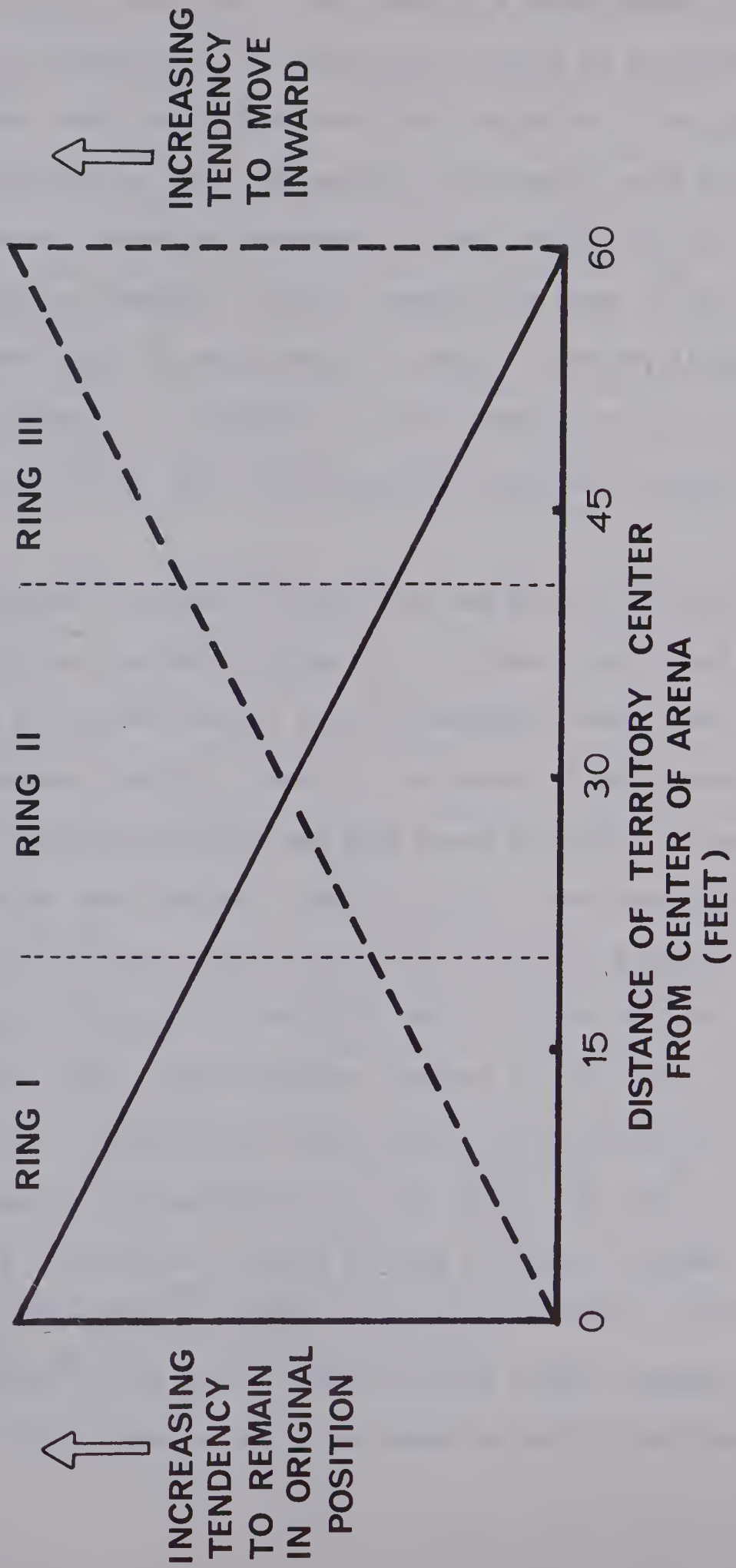
in early April, there were no cases where central males moved outward to the periphery of the arena. As the area taken up by central territories was reduced, intermediate males converged on the center of the arena as a unit while maintaining their relative positions. These males began to move inward individually only when central males had been reduced to one. Marginal males were generally opportunistic, moving directly into central positions when vacancies arose.

The fact that males moved toward the center of the arena while maintaining the original territorial arrangement, suggests that the center was a **preferred** position. If this was not the case and the males were merely moving toward the vacancies, the original territorial arrangement would not likely be preserved nor would the movements necessarily follow a pattern. To strengthen the argument that males are moving toward the center and not toward a vacancy, males should be removed centripetally on another set of arenas.

The tendency to remain in the same relative position and the tendency to move to a "better" position, that is, toward the center, appeared to be a function of the distance the territorial bird was from the geographic center of the arena. Central males apparently had a strong tendency to remain in their original central positions while marginal males appeared to have a strong tendency to move from the periphery of the arena to more central positions. In intermediate males, the tendencies seemed to be balanced. These differences are shown graphically in Figure 13.

Assuming that the center of the arena is a preferred area and

Figure 13. Hypothetical model showing the reaction of male sharp-tailed grouse to central vacancies in relation to the position they occupy on the arena.



and that territorial position on the arena is a consequence of the dominance of an individual, the males may be ranked in accordance to the distance their territories are from the center of the arena. If this was the case on Arenas BL and Apt, then males would have moved into central vacancies according to their social status, that is, when a male was removed, the male immediately lower in rank would have moved into the more central vacancy. However, if males have varying degrees of attachment to their territories (Fig. 13), they probably would not move into vacancies according to social rank.

Considering this possibility and from the general pattern of territorial shifts observed on Arena BL, it appears that A and the males in ring 1 may have been of similar dominance among themselves but dominant over all others on the arena. These males had attained the preferred position and none moved peripherally when central vacancies were created. Males in ring 2 were probably of lower rank than the more central males but of similar dominance among themselves because they tended to stay in their relative positions until central males had been reduced to one. The fact that the circular configuration of the ring of territories was generally preserved throughout most of the experiment (Fig. 9), probably was a consequence of males in ring 2 being of similar dominance and attempting to maintain positions as close as possible to the center of the arena. Males in ring 3 were probably subordinate to all others on the arena when the territorial map

was drawn on April 6. However, J, L, and D, which, in effect, bypassed ring 2 to occupy central positions, pose a problem. If they ranked lower than males in ring 2, why were they allowed to occupy central positions before any in ring 2? The fact that J maintained its central position for two days (Fig. 9), may mean that its dominance was equivalent to that of M and K in ring 2. However, there is no evidence that J and L would have maintained their central positions if removal had ceased after they moved centrally. Perhaps J and L would have been displaced by males in ring 2, forcing them to occupy their former peripheral positions if given enough time. D, which occupied a position in ring 1 on April 6 and 9, disappeared on April 10 and appeared again on April 29 to maintain a central position until it was shot on May 1 (Fig. 9). D may have been able to maintain its central position whereas J and L may not, because D's original rank was higher.

The fact that D was apparently accepted into the lekking flock after a 15 day absence, may mean that the social relationship among males on an arena is a type based on individual recognition. This type of relationship is common in domestic fowl (Masure and allee, 1934). If this type of social relationship exists in lekking species, then it is reasonable to assume that males attending an arena may be limited to the number that one male can "recognize". All others would be excluded.

CONCLUSION

It appeared that a significant portion of the male population of sharp-tailed grouse, studied at Camp Wainwright, Alberta, consisted of non-territorial juveniles. Non-territorial males were available during March and early April to occupy vacancies which were created in the social system on the arena. There was little evidence to show that inter-arena movements were common. Social organization within the lekking group was probably responsible for preventing surplus males from establishing territories on the arena. The social organization on the arena consisted of a hierarchal system superimposed on a system of territories. Dominance ranks appeared to be a function of the distance a territorial bird was from the center of the arena. Therefore, birds occupying positions equal distance from the center were of similar dominance.

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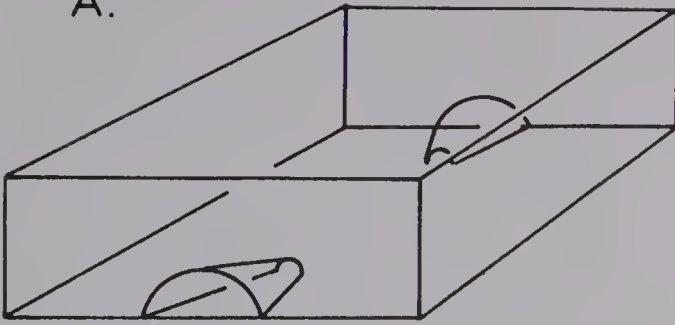
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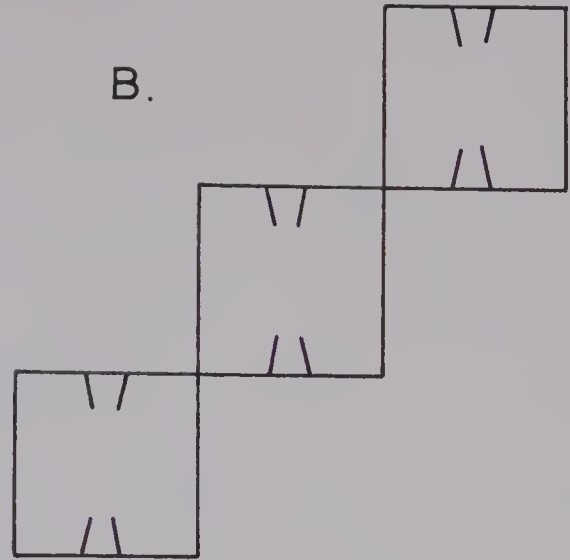
Appendix 1. Traps used to capture male sharp-tailed grouse on
arenas near Wainwright, Alberta.

A.



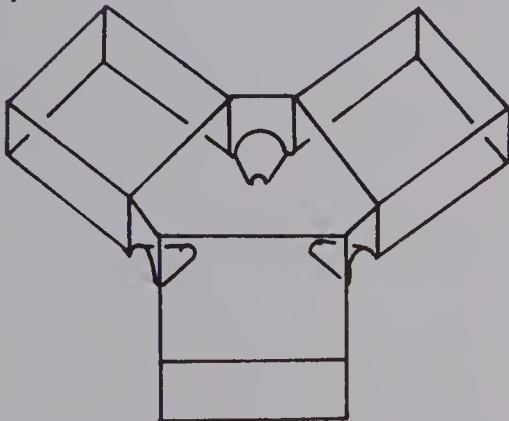
A. 6' X 6' X 18"
SIDES 1" MESH WIRE
TOP 1" NETTING

B.



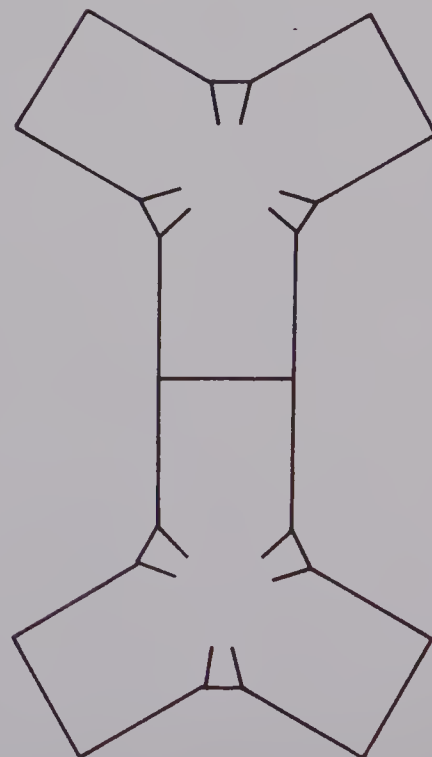
B. ARRANGEMENT OF THE TRAPS
ON AN ARENA

C.



C. SQUARE PORTION 4' X 4' X 18"
SIDES 1" MESH WIRE
TOP 1" NETTING

D.



D. ARRANGEMENT OF THE TRAPS
ON AN ARENA

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